RESEARCH ARTICLE

Population dynamics and growth of *Nassarius reticulatus* (Gastropoda: Nassariidae) in Rhosneigr (Anglesey, UK)

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Abstract Seasonal changes in catch rate, growth and mortality of *Nassarius reticulatus* from an intertidal lagoon and a wave-exposed beach at Rhosneigr (Anglesey, North Wales, UK) are described. The number of *N. reticulatus* caught in baited traps from the lagoon was significantly higher (>125 individuals trap^{-1}) during the summer (>18°C), than at <12°C (<65 individuals trap^{-1}), and the numbers caught in the lagoon were an order of magnitude greater than on the beach, >13 individuals trap^{-1} in July (>16°C), and <5 individuals trap^{-1} between December and April (<9.5°C). Predictions of shell growth attained by *N. reticulatus* annually in the lagoon using graphical modal progression analysis (MPA) of length frequency data, were similar to the growth of marked and recaptured lagoon *N. reticulatus*. Predictions of shell growth using computerised length frequency distribution analysis (LFDA), however, did not reflect the growth as accurately as MPA. Modal progression analysis demonstrated that *N. reticulatus* from the lagoon achieved a higher asymptotic maximum shell length (L_∞) and a lower growth constant (K) than animals from the beach. Shell growth was seasonal with growth of the lagoon individuals slowing down towards the end of September and resuming in early April, about a month later than the beach individuals. Mortality of *N. reticulatus* was greater during the summer, and survival was lower in the lagoon than on the beach. Recruitment patterns were similar in the lagoon and on the beach, and MPA and LFDA predicted that larval *N. reticulatus* settled between late summer and early autumn, with juveniles (7–8.9 mm) appearing in the population the following year, between February and April. Growth of male and female *N. reticulatus* in the laboratory was similar and was temperature and size dependent. The different growth patterns between *N. reticulatus* from the two habitats, predicted using MPA, were maintained when individuals were reared under laboratory conditions for ∼6 months; *N. reticulatus* <21 mm from the beach grew faster than individuals from the lagoon, although *N. reticulatus* >21 mm from the lagoon grew faster and attained a larger length (26 mm) than individuals from the beach (24 mm). Low food availability did not affect *N. reticulatus* survival in the laboratory but significantly suppressed shell growth.

Introduction

Scavenging gastropods are important components of subtidal and intertidal communities world-wide (Britton and Morton 1994). The population dynamics and growth of one species, *Nassarius reticulatus*, in European coastal waters have been studied. Length–frequency distribution analysis has been used to describe the population dynamics, recruitment, growth and migration patterns of *N. reticulatus* into Kvarnbukten Bay (Gullmar Fjord, Sweden) (Tallmark 1980). Whilst Lambeck (1984) has investigated the population dynamics of *N. reticulatus* in the recently colonised saline lake Grevelingen (SW Netherlands), and distinguished age-classes according to seasonal changes in modal size-classes within the size–frequency distributions. Barroso et al. (2005) estimated the age and growth of

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N. reticulatus in the Ria de Aveiro (Portugal) from an analysis of the population length–frequency distributions and from external shell growth rings and internal lines.

The demographic characteristics of a population, such as abundance, age structure, age specific growth rates and mortality reflect the ecology of a species and can provide information about the spatial and temporal extent of environmental stresses (Cerrato 1980). Population attributes can be deduced from size–frequency histograms, based on the premise that the sizes of individuals in each modal class approximate a normal distribution and that each modal class corresponds to a cohort and represents different age-classes determined at regular intervals (Morales-Nin 1992). However, the number of clearly defined modes can be reduced by poor recruitment in some years, variation in the duration of the breeding season, mortality and merging of older age groups (Cerrato 1980; Grant et al. 1987). The mixture of normal distributions in a population with overlapping cohorts can be dissected into its components by using either graphical methods that determine the area of cumulative frequency (e.g., Bhattacharya 1967), or computer methods based on a maximum likelihood statistical analysis (Grant et al. 1987; Morales-Nin 1992).

Determination of the number of age-classes and the longevity of a population using size–frequency analysis is problematic particularly when the older size-classes are poorly represented (Grant et al. 1987). One solution to the problem is to compare the modal size-class distributions with growth data derived from tagging or marking experiments (Grant et al. 1987). Several marking techniques have been used to measure shell growth in gastropods, including the incorporation of fluorescent markers, marking of the external shell surface using coloured dyes and numbered tags or drilling marks on the shell (Grant et al. 1987). Mark and recapture experiments were employed to determine seasonal growth in *N. reticulatus* (Tallmark 1980), *N. dorsatus* (McKillup and McKillup 1997) and *Ilyanassa obsoleta* (Curtis 1995). Growth can also be studied directly in organisms raised in captivity, where length progression can be followed throughout the rearing period, although growth under laboratory conditions is not always equivalent to growth in the natural environment (Morales-Nin 1992). The most commonly employed measure of growth for coiled gastropods is the change in shell length, measured from the apex to the furthermost point of the body whorl along the axis of coiling (Ekaratne and Crisp 1984).

Seasonal changes in seawater temperature, food availability and age have all been observed to affect the growth of nassariids. Elevated summer seawater temperatures correlated with an increase in the growth of *N. reticulatus* (Tallmark 1980; Lambeck 1984; Barroso et al. 2005), *N. festivus* (Morton and Chan 2004) and *Ilyanassa obsoleta* (Curtis 1995). McKillup and Buttler (1983) observed that

N. pauperatus adult size varied significantly with food availability in the field. Similarly, limited food supply retarded the growth of *N. dorsatus* (McKillup and McKillup 1997). Tallmark (1980) and Barroso et al. (2005) demonstrated that growth of *N. reticulatus* was fastest during the first years of life, but following sexual maturity growth rate decreased and became irregular.

In this paper the population dynamics of *N. reticulatus* from two contrasting habitats at Rhosneigr (Anglesey, UK), a sheltered intertidal lagoon and a wave-exposed subtidal beach are described. Two different methods, modal progression analysis (MPA) and length frequency distribution analysis (LFDA) are used to analyse the length frequency distributions, their results compared and evaluated and shell growth and mortality rates modelled using these data. Growth data obtained from laboratory experiments and from a field mark–recapture experiment are used to evaluate the validity of the growth patterns described using the MPA and LFDA methods and the environmental factors affecting shell growth of *N. reticulatus* are investigated.

Materials and methods

Sample collection

Seasonal variations in size and catches of *N. reticulatus* were investigated monthly between April 2002 and December 2003 at two different locations in Rhosneigr (Anglesey, North Wales, UK): a semi-enclosed rocky intertidal lagoon ($\sim$273 m^2) and a large area ($\sim$3,906 m^2) of a subtidal wave-exposed sandy beach (Fig. 1). An initial estimate of the index of dispersion ($I = 28.38$) of *N. reticulatus* suggested a clumped distribution (see Elliott 1977 for methodology), thus the density (unit area^{-1}) of individuals in the two habitats could not be accurately estimated. Instead population catch rates (catch unit effort^{-1}) were estimated from the number of individuals caught per trap during a 30 min period in a line of ten traps baited with mackerel. Total shell length (spire to the edge of the siphonal canal) was measured on site to the nearest 0.1 mm using vernier calipers and the *N. reticulatus* returned to the water following measurement.

Surface seawater temperature (SST) was recorded monthly during samplings using a digital thermometer and representative sediment samples collected once from both sites and analysed using the methods described by Folk (1968). The sediment from Rhosneigr beach was characterised as fine (mean = 2.58 Ø) moderately sorted sand (SD = 0.95 Ø), whereas in the intertidal lagoon it was coarse (mean = 0.29 Ø) and poorly sorted sand (SD = 1.65 Ø). The percentage silt and organic content was estimated to be 1.132 and 0.363% for the beach and 0.623
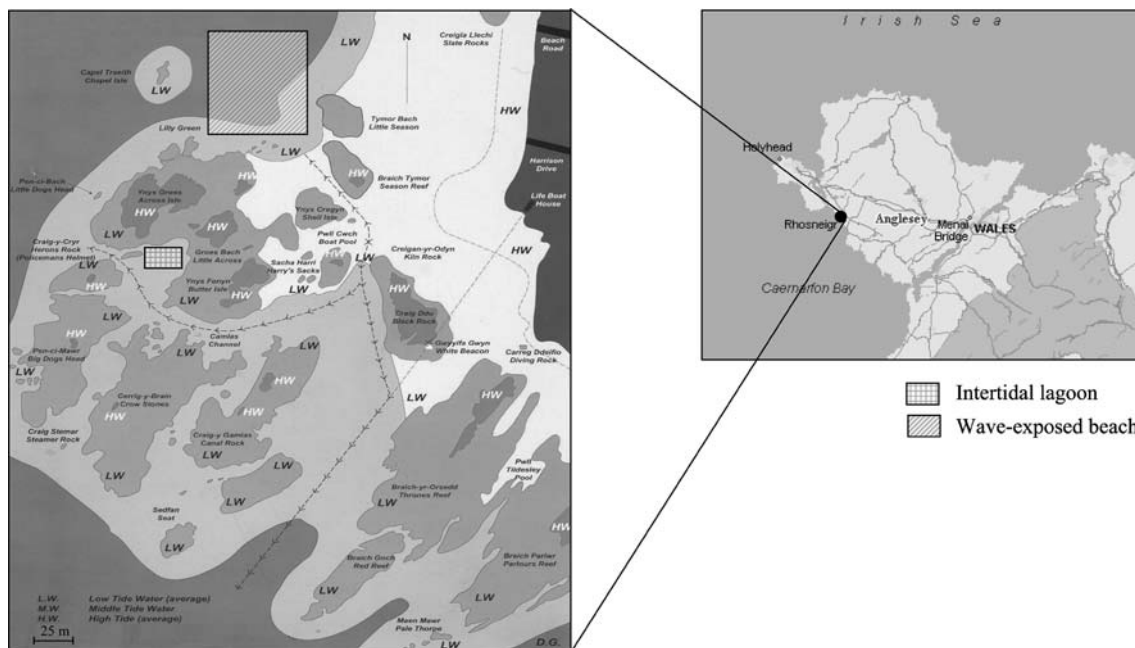
Fig. 1 Rhosneigr (Anglesey, North Wales). Location of the intertidal lagoon and wave-exposed beach sampling sites surveyed monthly from April 2002 to December 2003

and 0.654% for the lagoon sediment, respectively (Chatzinikolaou 2006). Sediment samples were collected from both sites every 2 months from April 2002 to April 2003 and examined carefully under the stereoscope for the presence of small *N. reticulatus*, in order to investigate if the use of baited traps as a sampling method failed to attract smaller individuals present in the area, however, no *N. reticulatus* <5 mm were found.

Modelling of growth and mortality
using length–frequency distribution data

The von Bertalanffy growth (VBG) equation $L(t) = L_\infty[1 - \exp[-K(t - t_0)]]$ predicts length as a function of age and can be used when growth is non-seasonal. In the present study a preliminary analysis of the length–frequency data indicated strong seasonal growth of *N. reticulatus* in both the intertidal lagoon and the subtidal beach, hence the data were modelled using Hoenig and Hanumara's (1982) seasonal version of the VBG model:

$$L(t) = L_\infty\left[1 - \exp\left[-K(t - t_0) + \left(C \times \frac{K}{2\pi}\right)\sin 2\pi(t - t_S)\right.\right.$$
$$\left.\left. - \left(C \times \frac{K}{2\pi}\right)\sin 2\pi(t_0 - t_S)\right]\right]$$

where L_∞ is the asymptotic maximum length, K is the growth rate, t_0 is the nominal age at which length is equal to zero, C is the relative amplitude of the seasonal

oscillations in growth rate ($0 \leq C \leq 1$), t_S is the phase of seasonal oscillations ($-0.5 \leq t_S \leq 0.5$).

The time of the year when growth is at its slowest is known as the winter point (WP = $t_S + \frac{1}{2}$). The parameters t_S and WP are "year units" and the beginning of a "year" is equivalent to the spawning period, which begins in May for *N. reticulatus* as eggs are usually laid at Rhosneigr and in the laboratory following this month (personal observation).

In situations where shell growth ceases for a period during the year then $C = 1$ and Pauly et al.'s (1992) model was used to describe the growth of the populations, according to the formula:

$$L(t) = L_\infty(1 - \exp(-q))$$

where

$$q = K(t' - t_0) + \frac{K}{Q}[\sin Q(t' - t_S)] - \frac{K}{Q}[\sin Q(t_0 - t_S)],$$

$$Q = \frac{2\pi}{1 - \mathrm{NGT}},$$

$t' = t_0$ for all $t \leq t_0$, and $t' = t_0 +$ total growth time between t_0 and t, for $t \geq t_0$.

The parameter NGT ($0 \leq \mathrm{NGT} < 1$) measures the length of time when no growth occurs. Annually the period of no growth commences at time $t_S + \frac{1}{2} - \frac{1}{2}$ NGT and finishes at time $t_S + \frac{1}{2} + \frac{1}{2}$ NGT.

Length–frequency distributions obtained during monthly sampling of the *N. reticulatus* populations from the intertidal lagoon and the subtidal beach were analysed using (1)

graphical modal progression analysis (MPA) (Bhattacharya 1967) to generate growth increment data produced from linkage of the means belonging to the same cohort and the VBG parameters were estimated using the method of Appeldoorn (1987) (FISAT II, version 1.2.0, FAO-ICLARM), and (2) length frequency distribution analysis (LFDA) which generates a growth curve from the "best fit" to the length–frequency data and calculates the VBG parameters using ELEFAN (LFDA, version 5.0, MRAG Ltd).

Total mortality rate (Z) is defined as the number of individuals that die during a season (month or year) in relation to the initial size of the population, and it was estimated using the equation $Z = \frac{K(L_\infty - L_{mean})}{L_\infty - L'}$ (Beverton and Holt 1956) (FISAT II) where L_∞ and K are the VBG growth parameters, L' is the cut-off length (the smallest length) and L_{mean} is the mean length. The percentage survival rate per annum was calculated as $e^{-Z} \times 100$.

Laboratory growth studies

Seventy-seven (8.9–28.9 mm) and 100 (7.6–28.6 mm) N. reticulatus were collected from the lagoon in May 2002 and the wave-exposed beach in June 2002, respectively. In the laboratory the N. reticulatus were divided into groups of five to six animals according to their size-class and location and labelled with a small numbered tag glued to their shells. The individuals were transferred into small plastic tanks (length, height, depth = $17 \times 10 \times 11$ cm) containing 3 cm of shell-sand sediment and provided with running seawater at ambient temperature. Seawater temperature was continuously monitored with a Tinytalk II temperature logger placed in one tank. Weekly, the N. reticulatus in each tank were fed with half of a freshly opened mussel Mytilus edulis. The shell length of each N. reticulatus was measured with vernier calipers (to the nearest 0.1 mm) at the beginning of the experiment (May and June 2002, respectively, for lagoon and beach individuals) and then monthly until December 2002. The growth rate ($R\%$) was estimated using the equation: $R\% = \frac{\ln L_1 - \ln L_0}{t} \times 100$, where $R\%$ is the relative daily growth rate, L_1 is the shell length (mm) after t (days) and L_0 is the initial shell length (mm). At the end of the experiment the sex of each individual was determined using Stroben et al.'s (1992) description. Shell growth was compared between seasons, between individuals in different size-classes, different sexes and different origins.

A further growth experiment studied the effects of limited food supply on N. reticulatus shell growth. One hundred and twelve N. reticulatus were collected from the intertidal lagoon in March 2004 and divided into two groups of 56 untagged individuals and maintained as described above. One group (9.7–28.1 mm) was fed weekly ("feeding" treatment) whilst the other group (10.1–27.5 mm) was fed monthly ("reduced feeding" treatment). Shell length and shell lip thickness of individuals were measured with vernier calipers (to the nearest 0.1 mm) monthly between March and August 2004.

Field growth studies

Five hundred and sixty-six N. reticulatus (7.9–31.4 mm) were collected from the lagoon on three occasions: 165 in June 2002, 101 in September 2002 and 300 during May 2003. Each individual was labelled with a numbered tag and its length measured before being released (within 24 h) back into the lagoon. N. reticulatus were recaptured opportunistically during routine monthly samplings over a total period of ∼2 years and their length re-measured before release. A mark and recapture experiment was not conducted on the wave-exposed beach, since the possibilities of recapture over the wider sampling area were considerably reduced. Measurements of the growth increment data obtained from the marked and recaptured individuals were analysed in order to estimate the VBG parameters L_∞ and K using Munro's (1982) method (FISAT II). The mark–recapture growth data were used to evaluate the validity of the growth patterns described using the MPA and LFDA methods, since the fit of the growth lines derived by these methods was not always accurate. The mark–recapture growth data were also used to compare growth of N. reticulatus in the intertidal lagoon with the growth of the regularly fed laboratory maintained individuals.

Results

Seasonal variation in catches of N. reticulatus

Similar seasonal patterns in SST were observed in the lagoon and on the wave-exposed beach. However in the lagoon SST was ∼3–6°C higher during the spring and summer months (March–August), and ∼2.4°C lower during winter (December–January) than on the wave-exposed beach (Fig. 2). Catches of N. reticulatus and SST were significantly correlated in both the lagoon and on the wave-exposed beach (Pearson correlation coefficients lagoon: $r = 0.787$, $P < 0.001$; beach: $r = 0.675$, $P = 0.002$). The major difference between the two localities was the number of N. reticulatus caught trap^{-1} (Fig. 2). Numbers caught in the lagoon were higher (>125 individuals trap^{-1}) during the warmer summer months (>18°C), than at <12°C (<65 individuals trap^{-1}) (Fig. 2). A broadly similar seasonal pattern was observed on the wave-exposed beach

where maximum numbers of *N. reticulatus* (>13 individuals trap^{-1}) were collected in July (SST > 16°C), and fewer *N. reticulatus* (<5 individuals trap^{-1}) were collected between December and April (SST < 9.5°C). The highest numbers of *N. reticulatus* from the wave-exposed beach (14.9 and 13.6 individuals trap^{-1} in July 2002 and 2003, respectively) were lower than the lowest numbers of *N. reticulatus* caught in the lagoon (29.7 individuals trap^{-1} in October 2003).

Estimation of the VBG parameters using modal progression analysis (MPA)

Modal progression analysis estimated that the VBG curve for *N. reticulatus* from the lagoon population had an asymptotic maximum length (L_∞) of 28.6 mm and a growth rate (K) of 0.70 year^{-1}. The relative amplitude of seasonal oscillations in growth rate $C = 0.78$ indicated a seasonal variation in growth. Growth was slowest at the winter point (WP) of 0.41 year units, equivalent to the end of September. The beginning of the convex segment of the sinusoidal oscillation (t_S) was at –0.09 year units, indicating that shell growth started to increase at the beginning of April. The growth curve constructed using MPA and fitted to the length–frequency data from the lagoon population

(Fig. 3) suggested that the larvae metamorphosed and settled during spring and summer, and the new recruits appeared into the population at a length of 7–8.9 mm between February and April the following year. This cohort reached a length of 15–16.9 mm by the end of September, 1 year following settlement. Shell growth did not cease completely during winter and *N. reticulatus* continued to grow slowly attaining a length of 19–20.9 mm the following April. Thus *N. reticulatus* reached a length of 23–24.9 mm, 25–26.9 mm and 27–28.9 mm in September, 2, 3 and 4 years, respectively, after their settlement.

The growth curve for the wave-exposed beach population, constructed using MPA, predicted an L_∞ of 25.5 mm, a K of 0.85 year^{-1} and a $C = 1$, indicating that growth ceased for a period of time. The winter point (WP) was estimated to be 0.28 year units, indicating that shell growth stopped after the middle of August and t_S was –0.22 year units, indicating that growth recommenced after mid-February. The MPA derived VBG curve for this population (Fig. 3) suggests that the larvae hatched and settled during spring and summer, and the new recruits appeared in the population between February and April the following year at a length of 7–8.9 mm. These 7–8.9-mm gastropods attained a length of 15–16.9 mm by the end of September, 1 year after settlement. Individuals grew slowly during the winter and reached a size of ~19–20.9 mm by the

Fig. 2 Seasonal variation in catches of *Nassarius reticulatus* (*bars* individuals collected trap^{-1} 30 min^{-1}) and seawater temperature (*line*) **a** in the intertidal lagoon and **b** on the wave-exposed beach at Rhosneigr. Note the different scales on the y axis (*Nassarius* trap^{-1}) in **a** and **b**
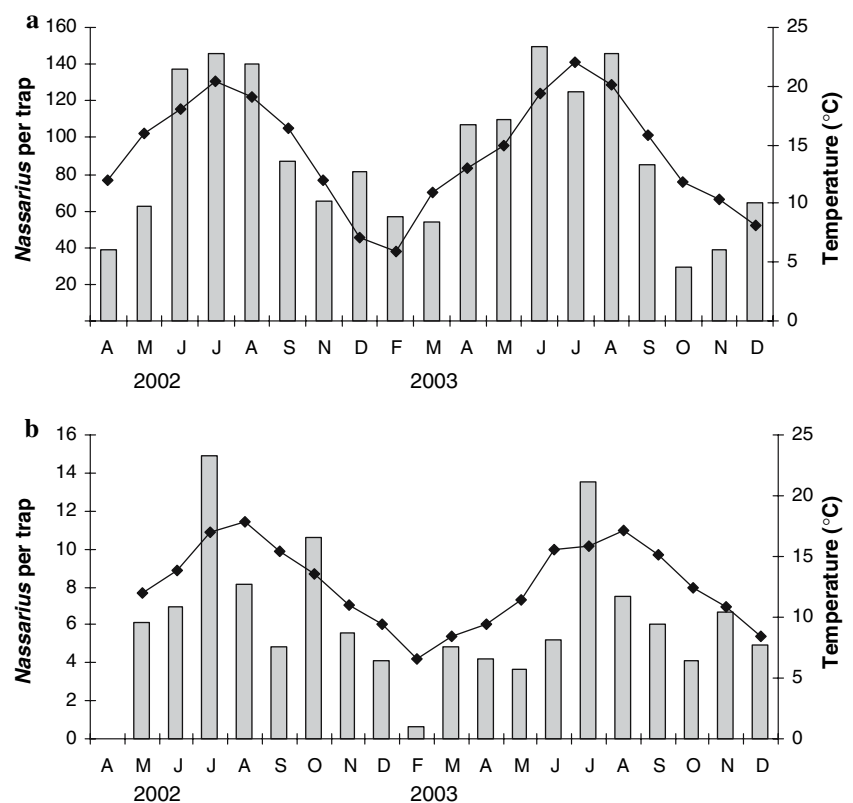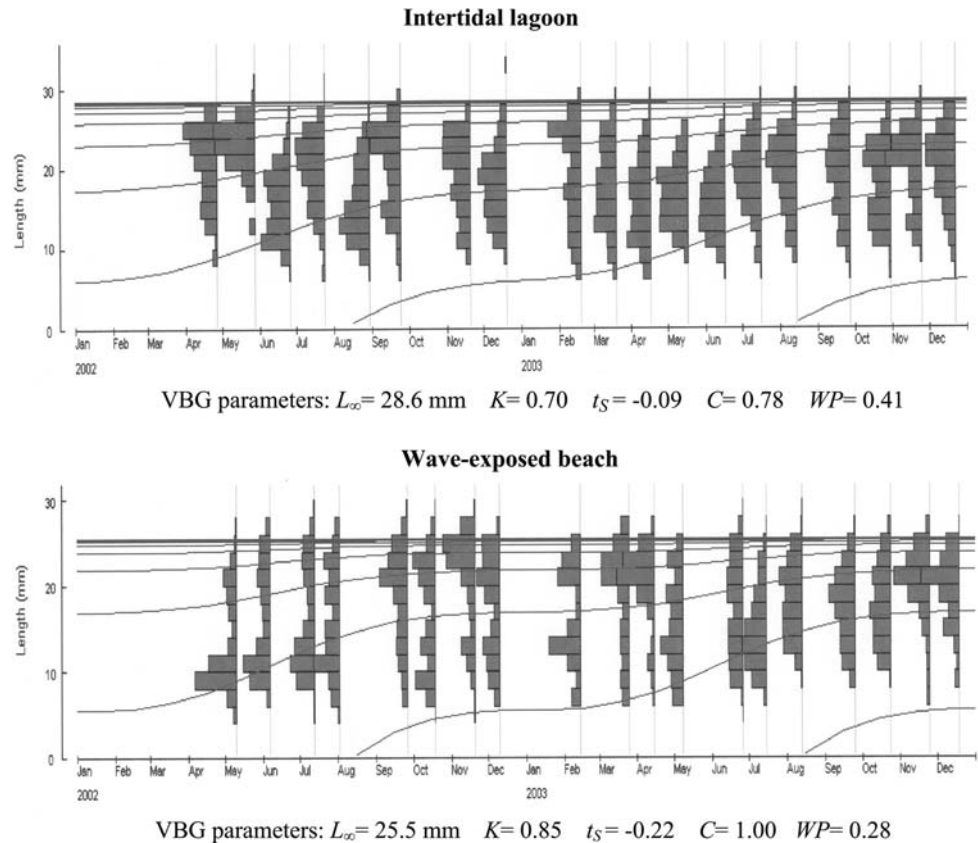
Fig. 3 Seasonal growth curves constructed from the von Bertalanffy parameters as determined by modal progression analysis (MPA) and fitted to the length–frequency data of the *Nassarius reticulatus* populations

Intertidal lagoon

VBG parameters: L_∞= 28.6 mm K= 0.70 t_S = -0.09 C= 0.78 WP= 0.41

Wave-exposed beach

VBG parameters: L_∞= 25.5 mm K= 0.85 t_S = -0.22 C= 1.00 WP= 0.28

following April and a size of 21–22.9 mm, 23–24.9 mm and 25–26.9 mm by September, 2, 3 and 4 years, respectively, after their settlement.
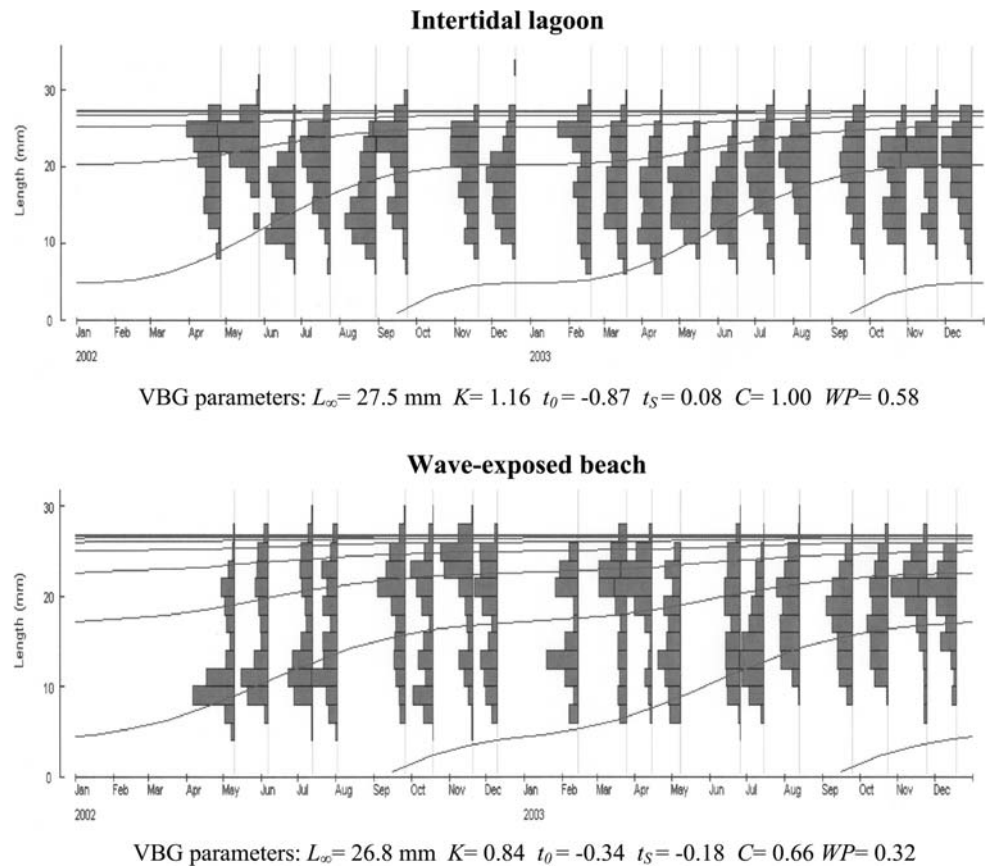
Estimation of the VBG parameters using length frequency distribution analysis (LFDA)

The LFDA method generated a VBG curve for the lagoon population with an L_∞ of 27.5 mm, a K of 1.16 year^{-1}, a t_0 of –0.87 year units, and a $C = 1$ indicating a strong seasonal variation in growth. The growth rate of *N. reticulatus* in the intertidal lagoon was slower during winter and ceased completely at a WP of 0.58 year units, equivalent to the end of November. The "no growth period" (NGT) extended between 0.51 and 0.66 year units, signifying that growth in the lagoon ceased between the beginning of November and the middle of December. The t_S was estimated to be 0.08 year units, indicating that growth started to increase at the end of May. The VBG curves fitted to the lagoon data using LFDA (Fig. 4) predicted that the larvae settled during spring and summer, and that new recruits (length 7–8.9 mm) appeared into the population between February and April the following year. These *N. reticulatus* reached 19–20.9 mm by the end of September, 1 year after settlement. Individuals grew very little during winter because of a

zero growth period, and attained a length of 21–22.9 mm by the following April. Growth resumed again in spring and they reached 25–26.9 mm and 27–28.9 mm in September, 2 and 3 years, respectively, after settlement.

The LFDA generated growth curve for the wave-exposed beach population was described by an L_∞ of 26.8 mm, a K of 0.84 year^{-1} and a t_0 of –0.34 year units. The C was 0.66, indicating that growth slowed down during winter but never ceased completely. The slowest growth rate was observed at a WP of 0.32 year units, which equates to the beginning of September. The t_S was at –0.18 year units, and indicated that growth began to increase after the end of February. The LFDA derived VBG curves (Fig. 4) predicted that larvae settled during spring and summer on the wave-exposed beach and that the new recruits appeared in the population at a size of 7–8.9 mm between February and April the following year. These *N. reticulatus* attained a size of 15–16.9 mm by the end of September, 1 year after settlement and then grew slowly during the winter, reaching a length of 19–20.9 mm by the following April. Growth rate increased after April and *N. reticulatus* reached a size of 21–22.9 mm and 25–26.9 mm by the end of September, 2 and 3 years, respectively, after their settlement. The LFDA predicted only three age-classes in the lagoon and beach populations whilst MPA predicted four age-classes in the populations.

Fig. 4 Seasonal growth curves constructed from the von Bertalanffy parameters as determined by length frequency distribution analysis (LFDA) and fitted to the length–frequency data of the *Nassarius reticulatus* populations

Intertidal lagoon

VBG parameters: $L_\infty = 27.5$ mm $K = 1.16$ $t_0 = -0.87$ $t_S = 0.08$ $C = 1.00$ $WP = 0.58$

Wave-exposed beach

VBG parameters: $L_\infty = 26.8$ mm $K = 0.84$ $t_0 = -0.34$ $t_S = -0.18$ $C = 0.66$ $WP = 0.32$

Comparison of the MPA and LFDA methods using mark–recapture growth data

Differences were observed between the VBG parameters estimated using the MPA and the LFDA methods (Figs. 3, 4). The LFDA indicated a lower L_∞ for the lagoon and a higher L_∞ for the wave-exposed beach populations than predicted using MPA. The estimated K for the lagoon individuals was higher using the LFDA analysis. The LFDA indicated that growth stopped completely (i.e., $C = 1$) for a period of time for the lagoon *N. reticulatus*, whilst the MPA suggested a complete cessation of growth for a period of time for the beach individuals. Using LFDA the period of slowest shell growth (WP) and the onset of spring shell growth (t_S) were shifted slightly later in the year compared with the results of MPA. In order to evaluate which of the two methods for analysing the length–frequency distributions more closely described the natural growth pattern of *N. reticulatus* in the lagoon, the growth data produced using the two methods (Figs. 3, 4) were compared with the growth data obtained over a period of 9–13 months from the marked and recaptured *N. reticulatus* (Table 1).

The LFDA generated VBG curves for the lagoon individuals (Fig. 4) predicted that the smallest *N. reticulatus*

appearing in the population in the spring (between February and April) at ∼7–8.9 mm, attained a size of 15–16.9 mm after only 3 months and reached a length of 21–22.9 mm 1 year later. However, according to the mark-recaptured data (Table 1) the 10.8 mm marked individuals had achieved a length of 15.1 mm when they were recaptured 11 months later, and the 15.5 mm individuals had attained a length of 20.7–21.4 mm after 11 more months. The LFDA method predicted a higher growth rate of *N. reticulatus* in the lagoon (shell length of 21–22.9 mm after just 1 year) compared with data obtained from marked and recaptured individuals, which required at least 2 years to grow to that size. Estimates of the growth rates of the larger (older) size-classes of *N. reticulatus* using LFDA predicted that the 19–20.9 mm individuals reached a size of 25–26.9 mm 1 year later. Similar estimates of growth were obtained from marked and recaptured animals of ∼21 mm which attained a size of 24.8–28.6 mm 1 year later, indicating that the LFDA method gave reasonable estimates only for the growth of the larger size-classes.

The MPA growth estimates were much closer to the observed growth increments from the marked and recaptured *N. reticulatus* than the LFDA estimations, for both small and large size-classes. For example, the VBG curves produced using MPA (Fig. 3) estimated that lagoon

Table 1 Increase in shell length of marked *Nassarius reticulatus* released on three occasions into the Rhosneigr lagoon and recaptured after a period of 9–13 months

Size class (mm)	Date 1	Length 1 (mm)	Date 2	Length 2 (mm)
First release—5 June 2002				
15–15.9	June 02	15.5	May 03	21.4
16–16.9	June 02	16.3	July 03	22.5
Second release—30 September 2002				
10–10.9	Sept 02	10.8	Aug 03	15.1
15–15.9	Sept 02	15.5	Aug 03	20.7
Third release—21 May 2003				
13–13.9	Dec 03	16.1	Sept 04	23.3
14–14.9	Aug 03	19.5	Sept 04	24.1
16–16.9	Aug 03	19.3	Aug 04	24.5
18–18.9	July 03	19.6	Aug 04	25.7
17–17.9	Sept 03	20.8	Sept 04	25.1
19–19.9	Aug 03	20.6	Aug 04	24.7
18–18.9	Sept 03	21.6	Sept 04	28.6
19–19.9	Sept 03	21.4	Sept 04	24.8

The shell length measurements are mean values from individuals of the same size class, and size class refers to the initial length of the whelks at the time of their first release into the lagoon

individuals with a size of ~7–8.9 mm when they first entered the population, reached a size of 15–16.9 mm after 7 months. Marked and recaptured *N. reticulatus* of 10.8 mm reached 15.1 mm after 11 months (Table 1). Growth of larger (older) size-classes was also well described by MPA: the MPA derived growth rates indicated that the 15–16.9 mm *N. reticulatus* reached a size of 19–20.9 mm in 7 months and a size of 23–24.9 mm in 1 year, whilst the 15.5 mm marked and recaptured *N. reticulatus* reached a size of 20.7–21.4 mm after 11 months, and the 16.1–16.3 mm marked individuals reached a size of 22.5–23.3 mm in 9–13 months. The MPA predicted that the 19–20.9 mm *N. reticulatus* reached 23–24.9 mm in 12 months, similar to the marked and recaptured individuals of 19.3–20.8 mm which attained a size of 24.1–25.7 mm in 12–13 months.

The growth increment data obtained from the marked and recaptured *N. reticulatus* were used to estimate the VBG parameters using the method of Munro (1982). Multiple recaptures were treated as independent measurements, and a growth increment was calculated for each period between successive recaptures. The calculated VBG parameters were similar to the MPA estimates; L_∞ was exactly the same (28.6 mm) whilst K from the mark–recapture data was 0.93 year^{-1}, higher than the MPA estimated value of 0.70 year^{-1}.

Mortality of *N. reticulatus*

A similar seasonal mortality pattern was observed in both habitats, although mortality was higher in the lagoon than on the wave-exposed beach (Fig. 5). Mortality was greatest during the late spring and early summer and lower during the autumn and winter, particularly for the lagoon population. The annual rate of total mortality was 0.778 for the lagoon population, and 0.577 for the beach population. Since there is no fishing mortality of *N. reticulatus* in Rhosneigr, total mortality will equal natural mortality within the population. The percentage survival rate annum^{-1} was 45.9% for the lagoon population and 56.2% for the wave-exposed beach population.

Growth of *N. reticulatus* under laboratory conditions

Comparison of seasonal growth rates of different size-classes

In order to eliminate any possible effect of gender or origin on growth, the monthly growth rate ($R\%$) of the laboratory *N. reticulatus* was calculated separately for female and male individuals collected from the two habitats. *N. reticulatus* of the same gender and origin were grouped into four size-classes <15 mm, 15–20 mm, 20–25 mm and >25 mm. The effects of ambient seawater temperature and size-class on growth were similar for both males and females irrespective of location (Table 2). Shell growth mainly occurred during the warm summer months (June–August), slowing down in September and October and ceasing completely during the colder winter months (November–December). Small *N. reticulatus* (between <15 and 20 mm) grew faster than individuals of 20–25 mm, whilst animals >25 mm did not increase in length. Smaller *N. reticulatus* grew for longer compared to large individuals that terminated their shell growth earlier in the year.

Shell growth of male and female *N. reticulatus*

The growth rate of all size-classes of female and male *N. reticulatus* was fastest between July and August, and these data were analysed separately and independently of location in order to eliminate any possible effect of origin on growth. Regression analysis between growth rate and initial shell length was used to eliminate the effect of size on growth rate. A significant negative correlation (Pearson correlation coefficient: lagoon females $r = -0.920$, $P < 0.001$; lagoon males $r = -0.918$, $P < 0.001$; beach females $r = -0.960$, $P < 0.001$; beach males $r = -0.947$, $P < 0.001$) and a significant linear regression (lagoon females $F = 170.57$,

Fig. 5 Seasonal mortality rate of *Nassarius reticulatus* from the intertidal lagoon (*closed symbols*) and the wave-exposed beach (*open symbols*) at Rhosneigr
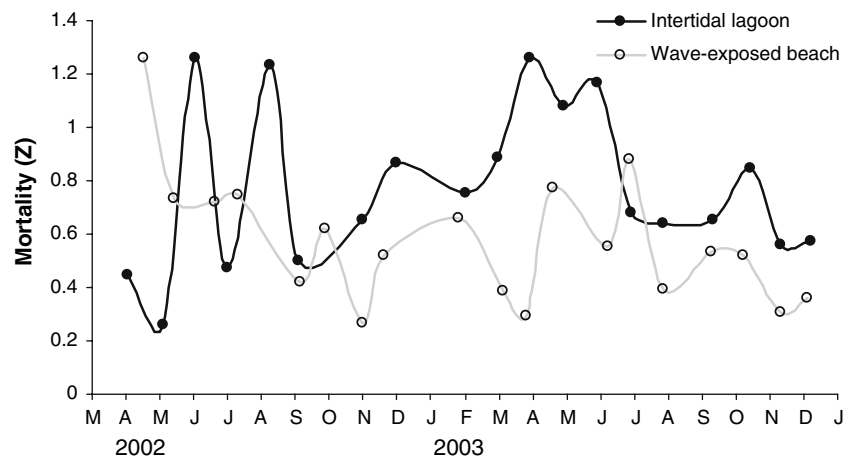
$P < 0.001$; lagoon males $F = 113.03$, $P < 0.001$; beach females $F = 537.54$, $P < 0.001$; beach males $F = 243.83$, $P < 0.001$) were found between growth rate and initial shell length for all groups of *N. reticulatus*, irrespective of their gender and origin (Fig. 6). General linear model (GLM) analysis demonstrated that shell growth was not significantly different between females and males from the lagoon (intercept $F = 0.46$, $P = 0.502$; slope $F = 1.52$, $P = 0.224$) or from the wave-exposed beach (GLM intercept: $F = 1.26$, $P = 0.266$; slope: $F = 3.15$, $P = 0.080$). However females from the lagoon and wave-exposed beach attained significantly larger mean shell lengths by the end of December 2002, 26.1 ($\pm$1.9) and 23.5 ($\pm$1.8) mm, respectively,

compared to males from the lagoon and wave-exposed beach that achieved a mean shell size of 24.1 ($\pm$1.3) and 22.0 ($\pm$1.5) mm, respectively (lagoon: Kruskal Wallis, $H = 21.54$, $P < 0.001$; beach: ANOVA, $F = 14.55$, $P < 0.001$).

Comparison between the growth rate of N. reticulatus originating from the intertidal lagoon and the wave-exposed beach

Having established that female and male growth was similar, both sexes were grouped together by location to

Table 2 Mean monthly growth rate (mm day^{-1}) ($R\%$) ($\pm$SE) of different size classes of female and male *Nassarius reticulatus* collected from the intertidal lagoon and the wave-exposed beach in Rhosneigr and maintained under laboratory conditions between June and December 2002

	Size class (mm)	N	June	July	August	September	October	November	December
Intertidal lagoon									
Females	<15	1	0.47 (NA)	0.47 (NA)	0.73 (NA)	0.70 (NA)	0.23 (NA)	NG	NG
	15–20	5	0.34 ($\pm$0.07)	0.36 ($\pm$0.04)	0.38 ($\pm$0.07)	0.22 ($\pm$0.05)	0.04 ($\pm$0.02)	NG	NG
	20–25	13	0.16 ($\pm$0.04)	0.16 ($\pm$0.04)	0.09 ($\pm$0.03)	0.02 ($\pm$0.02)	0.01 ($\pm$0.01)	NG	NG
	>25	14	0.01 ($\pm$0.01)	NG	NG	NG	NG	NG	NG
Males	<15	4	0.35 ($\pm$0.03)	0.40 ($\pm$0.04)	0.40 ($\pm$0.04)	0.35 ($\pm$0.03)	0.13 ($\pm$0.05)	NG	NG
	15–20	6	0.32 ($\pm$0.05)	0.38 ($\pm$0.03)	0.32 ($\pm$0.05)	0.08 ($\pm$0.04)	NG	NG	NG
	20–25	11	0.10 ($\pm$0.03)	0.09 ($\pm$0.03)	0.03 ($\pm$0.02)	NG	NG	NG	NG
	>25	2	NG	NG	NG	NG	NG	NG	NG
Wave-exposed beach									
Females	<15	21	ND	0.86 ($\pm$0.05)	0.59 ($\pm$0.03)	0.26 ($\pm$0.03)	0.06 ($\pm$0.02)	0.01 ($\pm$0.01)	NG
	15–20	6	ND	0.45 ($\pm$0.09)	0.38 ($\pm$0.03)	0.05 ($\pm$0.03)	NG	NG	NG
	20–25	17	ND	0.12 ($\pm$0.04)	0.08 ($\pm$0.03)	NG	NG	NG	NG
	>25	4	ND	NG	NG	NG	NG	NG	NG
Males	<15	19	ND	0.84 ($\pm$0.05)	0.58 ($\pm$0.03)	0.20 ($\pm$0.03)	0.02 ($\pm$0.01)	NG	NG
	15–20	6	ND	0.13 ($\pm$0.06)	0.08 ($\pm$0.04)	NG	NG	NG	NG
	20–25	5	ND	0.06 ($\pm$0.06)	0.02 ($\pm$0.02)	NG	NG	NG	NG

N size of sample, *NA* not applicable because sample size was 1, *NG* no growth, *ND* no data collected

compare the shell growth of *N. reticulatus* collected from the lagoon and the beach. Growth rate and initial shell length in the two habitats were significantly negatively correlated (Pearson correlation coefficient: lagoon $r = -0.901$, $P < 0.001$; beach $r = -0.947$, $P < 0.001$) and linearly related (lagoon $F = 323.45$, $P < 0.001$; beach $F = 831.82$, $P < 0.001$) (Fig. 7). GLM analysis identified a significant difference in the intercept ($F = 73.34$, $P < 0.001$) and the slope ($F = 72.75$, $P < 0.001$) of the regression between growth rate and initial shell size for individuals originating from the lagoon and the wave-exposed beach. Although the animals were maintained under identical laboratory conditions a different growth profile characterised the *N. reticulatus* originating from the two habitats. Small individuals (<21 mm) from the lagoon grew slower than those from the beach. By contrast the growth rate of larger lagoon individuals (>21 mm) was higher than beach animals of similar size. Lagoon individuals ceased shell growth when the animals reached a maximum size of ∼26 mm and beach individuals ceased growth at ∼24 mm. However, considerable variability between individuals regarding the size at which growth ceased was apparent. Small lagoon *N. reticulatus*, <15 and 15–20 mm, continued to grow

until October and September, respectively, whilst those from the beach stopped growing about a month earlier (Table 2).

The effect of limited food supply on N. reticulatus growth

A reduced feeding regime (fed once a month) had no significant impact on the survival of *N. reticulatus*, however, shell growth was completely suppressed. Shell length of the "food limited" individuals did not increase between March and August, however, there were significant seasonal differences in shell lip thickness for both the "fed" (Mood's median: $\chi^2 = 30.54$, $P < 0.001$) and the "food limited" individuals (Mood's median: $\chi^2 = 38.92$, $P < 0.001$) (Fig. 8). The shell lips of "fed" and "food limited" *N. reticulatus* were thinner during the warmer months (June–August), when shell deposition increased at the edge of the shell during the growing period. Thickness of shell lips was similar between "fed" and "food limited" individuals during the March–August period (Kruskal–Wallis: for March $H = 0.01$, $P = 0.965$; for April $H = 0.01$, $P = 0.914$; for June $H = 0.43$, $P = 0.510$; for August $H = 2.20$, $P = 0.138$).

Fig. 6 The relationship between growth rate (*R%*) (mm day^{-1}) and initial shell length (mm) for female (*circle*, *solid line*) and male (*cross symbol*, *dashed line*) *Nassarius reticulatus* collected from **a** the intertidal lagoon and **b** the wave-exposed beach and maintained in the laboratory
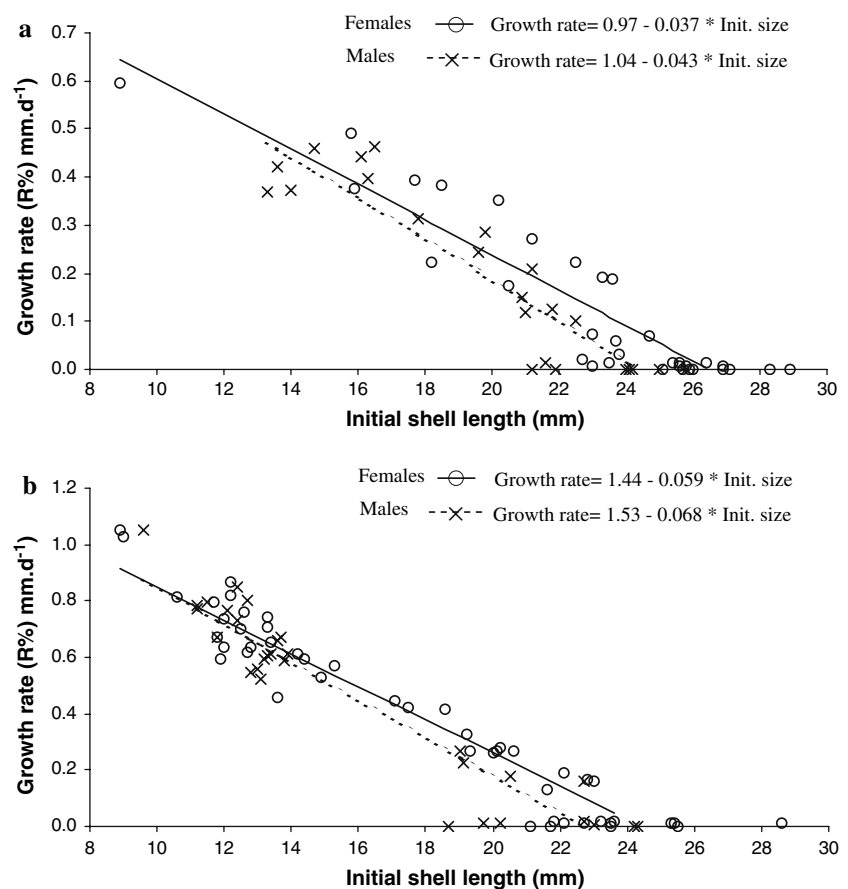
Comparison between the growth of lagoon and laboratory maintained N. reticulatus

When the summer growth rates of four size-classes (<15 mm, 15–20 mm, 20–25 mm and >25 mm) of marked and recaptured lagoon individuals were compared with the growth rates of similar sized *N. reticulatus* originating from the lagoon, but maintained in the laboratory and fed regularly (Table 3), it was observed that the smaller animals (<15 mm and 15–20 mm) grew significantly faster in the laboratory than in the lagoon (<15 mm: Kruskal Wallis $H = 8.69$, $P = 0.003$; 15–20 mm: ANOVA: $F = 108.58$, $P < 0.001$). However larger individuals (20–25 mm and >25 mm) had similar growth rates in the field and in the laboratory (Mood's median, class 20–25 mm: $\chi^2 = 0.47$, $P = 0.492$; class >25 mm: $\chi^2 = 3.38$, $P = 0.066$).

Discussion

N. reticulatus were caught more frequently in the lagoon and on the wave-exposed beach during the summer months when seawater temperatures were maximal than in the colder winter months. This observed seasonal pattern in catch rates resulted from an overall increase in activity and feeding response of *N. reticulatus* during the warmer months and a lack of activity and response towards the baited traps during the winter. Tallmark (1980) observed that more *N. reticulatus* were present in Kvarnbukten Bay (Sweden) during the summer months compared to the winter when the animals became immobile at temperatures below 4°C. Morton and Chan (2004) reported that *N. festivus* in Hong Kong were more active and more abundant during the summer. Whilst the traps had a degree of size selectivity and probably only trapped a fraction of the most active and hungry individuals in the population, both small and large animals were attracted to the carrion baits at all times of the year, albeit in lower numbers during the
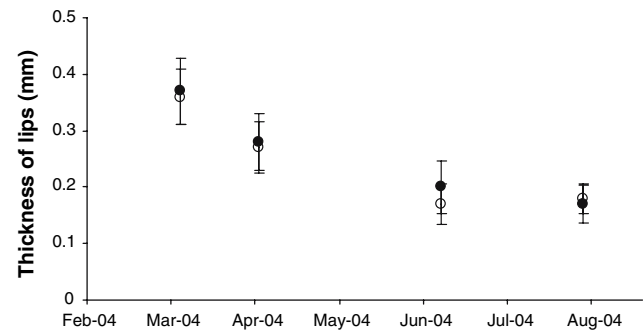

Fig. 8 Variation in mean shell lip thickness of *Nassarius reticulatus* fed weekly (fed, *closed symbol*) and fed once a month (food limited, *open symbol*) between March and August 2004. The *vertical error bars* represent the 95% confidence intervals (1.96 SE) of the means

winter. Trap selectivity does not compromise the use of length frequency methods for the determination of population growth as these methods are designed to estimate the seasonal growth rate (K) based on the younger fast-growing individuals, whereas the older and more mature animals, where growth has stopped, are used to estimate the maximum length that an individual can achieve (L_∞). Even if only a few mature animals are caught, the statistical software analyses the cohorts of the population and predicts the growth curves based on the data.

The Rhosneigr lagoon supported a significantly larger population of *N. reticulatus* than the wave-exposed beach and the greater numbers of individuals correlated with a 1.8-fold increase in organic content in the lagoon sediment compared to the wave-exposed beach. Population density of *N. reticulatus* was positively correlated with sediment organic content in Kvarnbukten Bay (Tallmark 1980), and in Hong Kong more *N. festivus* were associated with beaches receiving artisanal fisheries by-catches (Morton and Chan 2004). In Rhosneigr, falls of carrion are more likely to become trapped for longer in the wave-sheltered lagoon surrounded by rocks compared to the wave-exposed beach where carrion can be easily carried away by waves and

Fig. 7 The relationship between growth rate (*R%*) (mm day⁻¹) and initial shell length (mm) for *Nassarius reticulatus* originating from the intertidal lagoon (*open symbol*, *dashed line*) and wave-exposed beach (*closed symbol*, *solid line*) and maintained under laboratory conditions
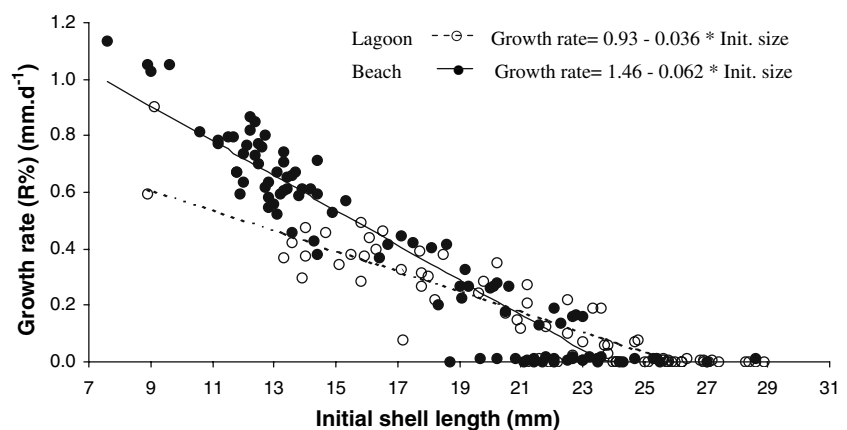
Table 3 Comparison of the mean growth rates ($R\%$) (mm day^{-1}) (±SE) of different size classes of *Nassarius reticulatus* originating from the intertidal lagoon and maintained under laboratory conditions between June and September, and the $R\%$ (±SE) of marked whelks released into the Rhosneigr lagoon and recaptured between May and September

Size class (mm)	Laboratory maintained		Marked and recaptured	
	Sample size (N)	$R\%$ (±SE) (mm day^{-1})	Sample size (N)	R% (±SE) (mm day^{-1})
<15	8	0.41 (±0.04)	5	0.13 (±0.03)
15–20	18	0.29 (±0.02)	42	0.10 (±0.01)
20–25	28	0.08 (±0.01)	42	0.09 (±0.01)
>25	23	0.01 (±0.002)	5	0.08 (±0.04)

currents. The sheltered location of the lagoon and elevated summer seawater temperatures together with the higher organic sediment content probably conferred a greater potential for successful recruitment and growth of *N. reticulatus*. McKillup et al. (1993) suggested that the elevated seawater temperatures in extensive water pools that formed during low tide on a sand flat in the Gulf of St Vincent (South Australia), enhanced the growth and survival of *N. pauperatus* larvae that were trapped there.

Natural mortality varied seasonally with higher mortality rates during the spring and summer months. Elevated seawater temperatures (22°C) during the summer, together with an increased physiological demand and greater reproductive effort were probably responsible for the increase in mortality compared to the winter. Spight (1982) demonstrated a marked seasonal variability in mortality rates of *Thais emarginata* and *T. lamellosa* in San Juan Island (Washington), most individuals dying during the summer when the environmental conditions were more stressful. Mortality rates were higher for *N. reticulatus* in the intertidal lagoon compared with individuals in the subtidal beach. *N. reticulatus* inhabiting the subtidal wave-exposed beach experienced a smaller range of seawater temperatures (6.6°C in winter to 17.1°C in summer) thus resulting in a lower mortality rate compared with the intertidal lagoon (5.9–22°C). Furthermore, crab-induced mortality may also have contributed to the higher mortality rate in the lagoon because predatory crabs *Carcinus maenas* were more abundant around the carrion baited traps in this habitat (Chatzinikolaou 2006).

The VBG parameters obtained from the graphical MPA and the computerised LFDA methods were not in complete agreement. The pattern of shell growth estimated using MPA was closer to that obtained from measurements of shell growth from the marked and recaptured individuals. The LFDA method is designed to analyse the growth of fish populations in which the movement of individuals will average the impact of environmental variations (Grant et al. 1987). Therefore, the LFDA may not be completely appropriate for analysing data from relatively non-mobile

N. reticulatus populations where large variations in annual recruitment can occur, or where growth rates may fluctuate with time due to the effect of population density on growth (Grant et al. 1987). The MPA method predicted that individuals from the lagoon had a slower growth rate (i.e., a lower K) than those from the wave-exposed beach. *N. reticulatus* growth is slower in high density populations due to increased intra-specific competition (Lambeck 1984) and since the density of individuals was higher in the lagoon than in the wave-exposed beach, this might account for the observed lower growth rate of the lagoon population. The presence of a large predatory crab population inhabiting the lagoon during the summer may have influenced growth. In the presence of crabs thickening of the gastropod shell is promoted at the expense of linear growth to strengthen the shell (Wellington and Kuris 1983). Since there is a maximum rate at which calcification can occur (Trussell and Smith 2000), a greater energy investment in shell thickening may account for the lower growth rate (measured as shell length) of the lagoon population. Although *N. reticulatus* had a slower growth rate in the lagoon than in the wave-exposed beach, the L_∞ of the lagoon population was higher resulting in larger animals. The formation of larger shells in sheltered environments offers effective protection against predation (Parsons 1997) since large shells require more energy to break them (Juanes 1992) and their relative shell strength increases roughly with the 1/3 power of shell length (Tokeshi et al. 2000).

N. reticulatus in the lagoon continued to accrete shell during August (SST 19–20.1°C), their growth only decreasing after the end of September when the SST dropped to ∼16°C. Growth of the wave-exposed beach *N. reticulatus*, however, ceased a month earlier, i.e., mid-August, when the SST had fallen to between 16.0 and 17.1°C. In the spring, growth of the beach individuals began in mid-February (SST 6.6–8.5°C) earlier than in the lagoon, where growth started in early April (SST 13°C). A possible reason for the delay in the onset of growth in the lagoon *N. reticulatus* might be that they had experienced a

SST <7.1°C for a 3-month period during the winter, thus lowering their metabolism, whilst the beach individuals had experienced a SST of <8.5°C only in February and their metabolism was not affected to the same extend as their lagoon conspecifics.

The smallest *N. reticulatus* collected by baited traps from the intertidal lagoon and wave-exposed beach were 7–8.9 mm and 5–6.9 mm, respectively, suggesting that individuals <5 mm were either not present in the population or were not attracted to the carrion offered in the traps. However, juvenile *N. reticulatus* were attracted and actively fed on mackerel and *Mytilus edulis* flesh as observed under laboratory conditions (Chatzinikolaou and Richardson 2007). In addition, the absence of smaller *N. reticulatus* in the sediment samples examined regularly indicated that young individuals were not present in the adult populations. Barroso and Moreira (1998) noted a lack of *N. reticulatus* <6.5 mm in samples of sediment obtained seasonally from the Ria de Aveiro (Portugal), and speculated that there may be separate nursery sites for settlement from where the juveniles migrated and recruited into the main population when they were almost 1-year old. The VBG curves fitted to the length–frequency data predicted that the *N. reticulatus* larvae settled during the spring and summer in both the lagoon and the beach populations, and appeared as part of the population between February and April the following year at a length of 7–8.9 mm. Barroso et al. (2005) proposed a single annual recruitment for *N. reticulatus* in the Ria de Aveiro (Portugal), where larvae hatched from their egg cases in early spring, settled in late spring and were part of the population at a size of 5 mm by September of the same year. Lambeck (1984) reported that recruitment of *N. reticulatus* in Grevelingen (SW Netherlands) was annual, whereas Tallmark (1980) indicated a non-annual recruitment of the same species into Kvarnbukten Bay (Sweden) where recruitment only occurred three times during the 5-year study period. *N. reticulatus* from Rhosneigr grew rapidly and attained a length of 15–16.9 mm after two growing seasons, a size similar to that obtained by *N. reticulatus* in lake

Grevelingen (Lambeck 1984) (see Table 4). Both Tallmark (1980) and Barroso et al. (2005) found that in 2 years *N. reticulatus* only achieved a length of 11 mm in Kvarnbukten Bay and 12.1–14.5 mm in Ria de Aveiro, respectively. The lengths of older (fourth and fifth year) age-classes of *N. reticulatus* from Rhosneigr beach were, however, similar to the estimated lengths of individuals from Portugal (Table 4).

Field monitored and laboratory maintained *N. reticulatus* displayed a strong seasonal growth pattern, with highest growth rates achieved during the summer, slower growth during the autumn, and growth cessation during the winter. Seasonal patterns of shell growth have been observed for nassarids elsewhere, for example *N. reticulatus* in lake Grevelingen began growing at ∼14°C in mid-April and grew rapidly during the summer (Lambeck 1984) and *N. reticulatus* in the Ria de Aveiro displayed minimum growth during the winter and maximum growth during the summer (Barroso et al. 2005). Hong Kong populations of *N. festivus* displayed seasonal growth (Morton and Chan 2004) and the observed decrease in growth rate of *N. obsoletus* in Falmouth (MA, USA) was attributed to the cessation of feeding activity during winter due to a decrease in food availability and low seawater temperatures (Scheltema 1964).

Size dependent growth of *N. reticulatus* was observed in smaller individuals (<15 mm, 15–20 mm) growing faster than large animals (20–25 mm). Small *N. reticulatus* (<15 mm) continued to grow in October, whereas larger individuals (15–20 mm and 20–25 mm) stopped growing earlier at the end of August. Large *N. reticulatus* (>25 mm) showed no obvious shell growth even during the summer months and this is attributed to the onset of sexual maturity as energy is diverted from shell growth to reproduction. Tallmark (1980) reported that growth of *N. reticulatus* in Sweden slowed and became irregular after the fourth year when individuals became sexually mature, and ceased when they were >20 mm. Similarly, in the Ria de Aveiro *N. reticulatus* grew for the first 5 years depositing only a small increment of shell in the following

Table 4 Comparison of the Rhosneigr *Nassarius reticulatus* length-at-age data predicted using modal progression analysis (MPA) of length frequency distributions with modal class data from other locations

Predicted shell length attained each year (mm)					Locality	Reference
First year	Second year	Third year	Fourth year	Fifth year		
7–8.9	15–16.9	23–24.9	25–26.9	27–28.9	Rhosneigr lagoon, Anglesey, UK	Present study
7–8.9	15–16.9	21–22.9	23–24.9	25–26.9	Rhosneigr beach, Anglesey, UK	Present study
5.5	11	16.5	NA	NA	Gullmar fjord, Sweden	Tallmark (1980)
6.8	16	NA	NA	NA	Grevelingen lake, The Netherlands	Lambeck (1984)
6.7–7.8	12.1–14.5	18–19.5	22.7–23.6	26.1–26.9	Ria de Aveiro, Portugal	Barroso et al. (2005)

NA not available

years (Barroso et al. 2005). In the present study, small *N. reticulatus* (<15 mm, 15–20 mm) reared in the laboratory with a regular supply of food, had a significantly higher growth rate than marked and recaptured individuals of similar size that were monitored in the intertidal lagoon. Large individuals (>20 mm) maintained under laboratory conditions and fed to excess, however, had similar growth rates to marked and recaptured *N. reticulatus* monitored in the field, since sexually mature animals invest most of the absorbed energy into reproductive activity and not into shell growth. Ota and Tokeshi (2000) observed that *Japeuthria ferrea* and *J. cingulata* rarely achieved their potential maximum growth in the field because of insufficient food, competition and environmental constraints.

In the present study shell growth rates were similar between male and female *N. reticulatus* reared under laboratory conditions. However, females attained a significantly larger length than males, indicating that the female *N. reticulatus* grow for a longer period during their life time. A possible explanation could be either that females live longer than males, or that males mature and terminate their growth earlier than females, however, further research on this subject is necessary. Barroso et al. (2005) also demonstrated that female *N. reticulatus* attained a significantly larger size than males in Portugal. Similar growth rates between males and females have also been reported for other gastropod species such as *Ilyanassa obsoleta* (Curtis 1995) and *Concholepas concholepas* (Rabi and Maravi 1991).

The differences observed following MPA between the growth patterns of *N. reticulatus* in the lagoon and on the beach were also maintained when the animals were transferred in the laboratory and kept under identical conditions for a period of 6–7 months. Lagoon individuals grew significantly slower during the first stages of life, they grew for a longer period within the year, the larger size-classes maintained a higher growth rate, and they reached a larger length than the beach individuals. Morton and Chan (2004) observed significantly different growth rates of *N. festivus* in three different habitats and similarly noted that the same differences in growth rates were maintained when they were transferred into the laboratory. The reasons for this are currently unknown.

Survival of *N. reticulatus* in the laboratory was not affected by limiting the food supply, although shell growth became completely suppressed. Tallmark (1980) reported that 65% of *N. reticulatus* survived but did not grow when they were starved for 5 months. In the present study both regularly fed and food limited individuals formed a thinner shell lip (margin) during the summer (June–August), and thickened the shell margin when shell deposition slowed during the winter. In Portugal *N. reticulatus* developed a thick shell lip with associated teeth during the winter, whereas in the summer the lips were thin and the teeth

disappeared (Barroso et al. 2005). In the current study although food-limited individuals did not appear to increase in length, their shell lips were thin during the summer and thickened during the winter. Presumably low availability of food provided insufficient energy for the shell to measurably increase in length, although deposition of shell material on the shell edge of food limited individuals did occur as they were able to thicken their shell lip during winter.

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